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Ingestion of mineral soil/litter mixtures and faecal pellet production in the southern African millipede *Alloporus uncinatus* (Attems)

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Summary. Palatability and food preference experiments are described in which the savanna millipede *Alloporus uncinatus* was given food which consisted of ashed mineral soil and mechanically ground leaf litter alone and in mixtures of 25%, 50% and 75% mineral soil by volume. Ingestion, retention time and the production of faecal pellets were measured. In the palatability experiment food treatment, body mass and the sex of the animal all had significant effects on one or more of the measured variables. Mixtures of mineral soil and leaf litter (25% and 50% soil) were ingested at similar rates to pure litter but retention time was shorter in mixtures. Individual *A. uncinatus* also ingested between 26 and 43% of the ashed soil. There was a non-random selection of foods in the preference experiment with high organic matter foods being preferred. However, a significant proportion of all foods presented was ingested including mineral soil. Explanations for the ingestion of ashed soil are considered and measured ingestion rates compared with published data for other millipede species. The implications of potential food selectivity on faecal pellet production and subsequently leaf litter turnover by millipedes in natural habitats are considered.

Key words: Feeding, faeces, *Alloporus uncinatus*, Diplopoda

Introduction

Millipede species of the Spirostreptidae and Odontopygidae families are particularly abundant in the wooded savanna ecosystems of southern Africa (Lawrence, 1984) and are conspicuous during periods of surface activity (Dangerfield & Telford, 1991). In most of these species adults are of medium to large size (2–20 g body mass) and form a large proportion of the detritivore faunal biomass in many savanna habitats (Malaisse, 1978; Dangerfield, 1990).

Although millipedes are known to eat a wide variety of foods they are generally consumers of decomposing plant tissue including leaf litter (Wooten & Crawford, 1975; Kheirallah, 1979), fallen fruits, fungal fruiting bodies (Dangerfield & Telford, In Press) and even dead invertebrates (Dangerfield, pers. obs.). Despite this generality individuals do appear to make a positive selection of food items (Kheirallah, 1979; Pobozsny, 1986).

Previous studies of millipede feeding ecology have noted the ingestion of mineral soil as a component of the diet (Bocock & Heath, 1966; Saito, 1968; Kheirallah, 1979) and in the present study faecal material collected from animals feeding in the field contained some mineral soil. Soil may be consumed as a consequence of ingesting small particles of leaf litter that are not easily separated from mineral soil. Small fractions of leaf litter are often well decayed and palatable to detritivores (Hassall & Rushton, 1984) yet they occur in the lower litter horizons and as a consequence become mixed with the mineral fractions, particularly in sandy soils. In these situations, the shovelling action of millipede mouthparts (Kohler, et al., In prep.) would result in the ingestion of mineral soil "by accident" and its presence in the diet could have no functional significance.

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An alternative hypothesis is that mineral soil acts as roughage and decreases the retention time of ingested material. This would be of value to animals that have poor assimilation efficiencies or consume poor quality foods (Sibly, 1981). A rapid turnover may often provide more nutritional benefit than extended digestion of poor quality material, but would in turn require high ingestion rates.

A second alternative is that mineral soil may provide nutrients, particularly salt for the production of the exoskeleton, that are not available in other food sources (Kime & Wauthy, 1984). This may be an explanation for the phenomenon of large aggregations of millipedes feeding on mineral soil (Dangerfield & Telford, In Press).

In this paper laboratory experiments are described in which the widespread savanna spirostrepsid *Alloporus uncinatus* (Attems) was given food that varied in the proportions of mineral soil to organic material to test the hypothesis that the amount of mineral soil in the food influences ingestion rate, retention time and faecal pellet production. The ability of *A. uncinatus* to discriminate between different mixtures of organic matter and mineral soil was also determined by measuring the degree of selectivity in a food preference experiment. The consequences of any selectivity on rates of ingestion and faecal pellet production are considered, particularly in terms of the influence of *A. uncinatus* on nutrient cycling.

Materials and Methods

Collection of animals

Alloporus uncinatus is a common and widespread species which occurs in natural woodlands, plantations, savannas and suburban gardens throughout southern Africa. Individuals were collected from a population inhabiting deciduous riparian woodland at Mazowe Dam, 35 km north of Harare, Zimbabwe (17° 30′ S, 30° 57′ E). This site was immediately downstream of a major dam on the steep banks of the Mazowe river. The vegetation was dominated by the canopy tree *Celtis africana* (N. L. Burm.) with a dense bush layer *(Teralobium stellatum)* and sparse ground cover. Throughout the rainy season (November to April) *A. uncinatus* was abundant and surface active. Animals used in the experiment were collected by hand on 21st March 1988.

Preparation of animals

Each animal was weighed and its sex recorded before being placed in separate plastic containers (10 cm diameter × 13 cm deep). The animals were maintained at a constant temperature (20 ± 5 °C) without food for 18 days until no further faecal pellets were produced. At this time it was assumed that the gut of each animal was empty.

Preparation of foods

The food presented was mixtures of mineral soil and organic matter. Soil typical of the region (a granite derived alfisol) was ashed in a muffle furnace at 650 °C for 24 hours to burn off all organic matter and thus provide a food type of no energetic value to the animals. This material was mixed with well decayed leaf litter from the savanna trees *Brachystegia spiciformis* (Benth.) and *Julbernardia globiflora* (Troupin) which had been finely ground (<0.75 mm). This organic material was of uniform if not optimal quality and was readily ingested by *A. uncinatus* in separate laboratory cultures.

Palatability experiment

The leaf material was mixed with the mineral soil in proportions of 0, 25, 50, 75 and 100% by dry volume. 70 animals were randomly assigned to each of these five food treatments to give 14 replicates of each treatment. Food was presented in a 3 cm diameter plastic dish for a three week period. The mean dry mass (mg ± 1 s. e.) of food in each replicate was 6.60 ± 0.17 in the 100% soil treatment, 5.85 ± 0.06 for 75% soil, 4.98 ± 0.05 for 50% soil, 3.94 ± 0.05 for 25% soil and 2.81 ± 0.04 for organic material only. Observations of laboratory cultures showed that *A. uncinatus* prefers moist litter, therefore, a daily addition of 1 ml of distilled water was made to each food dish with an automatic pipette.

Food preference experiment

The same mixtures of leaf litter and ashed soil as those used in the palatability experiment were presented separately to 12 female and 13 male *A. uncinatus*. Each food type was placed in a 3 cm diameter plastic dish which was in turn placed in the base of a clean petri-dish. The petri-dish collected any food disturbed from the feeding dish but not eaten by the millipede and did not obstruct the movement of the animal. The five petri-dishes were fixed with "Blu-tac" to the base of a 20 cm × 30 cm × 5 cm plastic tray. A second tray was inverted over the first to produce an enclosed unit. As in the palatability experiment 1 ml of distilled water was added to each food dish every 24 hours for the duration of the experiment (14 days).

Measurements and analysis of results

At the end of both experiments the food remaining in each replicate was dried for 24 hours at 70 °C and weighed. Ingestion was expressed as the percentage dry mass of food eaten during each experiment. The daily production of faecal pellets by each animal was recorded and retention time was measured as the time taken to produce the first pellet. Pellet production rate was expressed as the number of pellets per day from the start of pellet production to the termination of the experiment. Faecal pellets are cylindrical in shape which allowed pellet volume (mm^3) to be estimated from measurements of pellet length and width made under a dissecting microscope fitted with a Wild graticule eyepiece (1 micrometer unit = 0.076 mm). Data on ingestion, retention time, pellet production rate and pellet volume were each analysed with a multivariate analysis of covariance model using SYSTAT (Wilkinson, 1986). This analysis tested for any effects of treatment and sex while holding constant the effects of body mass.

Results

Palatability

The highest percentage of food eaten in the three week period (82.7%) was by females offered food containing 25% soil, yet in all treatments significant amounts of food were ingested (fig. 1 (a)). All the food treatments appeared to be palatable. Even in the 100% soil treatment a loss of 34.5% represents 2.28 mg of dry soil eaten. Across all treatments body mass had a significant influence on ingestion and when this effect was statistically removed there were significant differences in ingestion between the treatments, but the sex of the animal had no effect (table 1).

Animals were starved before the start of the experiment and only used if they had not produced faecal material for at least 7 days. The pellets recorded in the experiment were assumed to be from the current feeding event and therefore, the time taken to produce the first pellet was considered an accurate measure of retention time. Some females in the 50% soil treatment produced pellets after only 2 days, whilst animals fed soil only produced no pellets even though some food was ingested. The mean time to first pellet production by males and females in all treatments is shown in fig. 1 (b). Mixtures of soil and organic

Table 1. Analysis of covariance table for ingestion (percentage dry mass of food eaten) by *Alloporus uncinatus* in five food treatments

Source	d. f.	SS	MS	F-ratio
Treatments	4	3528.18	882.04	19.25***
Sex	1	0.14	0.14	0.01^{ns}
Live mass	1	553.52	553.52	12.07***
Error	32	1466.61	45.83	

In this and subsequent tables: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ and ^{ns} not significant. Percentages were transformed to arcsine for use in the model and an F-test for heterogeneity in between group slopes was not significant

material decreased retention time and although treatment effects were significant there was no significant effect of sex or body mass (table 2).

The mean number of faecal pellets produced per day by males and females in each food treatment is shown in fig. 1 (c). Although there appears to be differences between treatments and sex these were not significant (table 3). There was considerable variance between individuals within treatments, for example the range in mean pellet production rate for males in the 50% soil treatment was 0.55 to 3.21 pellets per day.

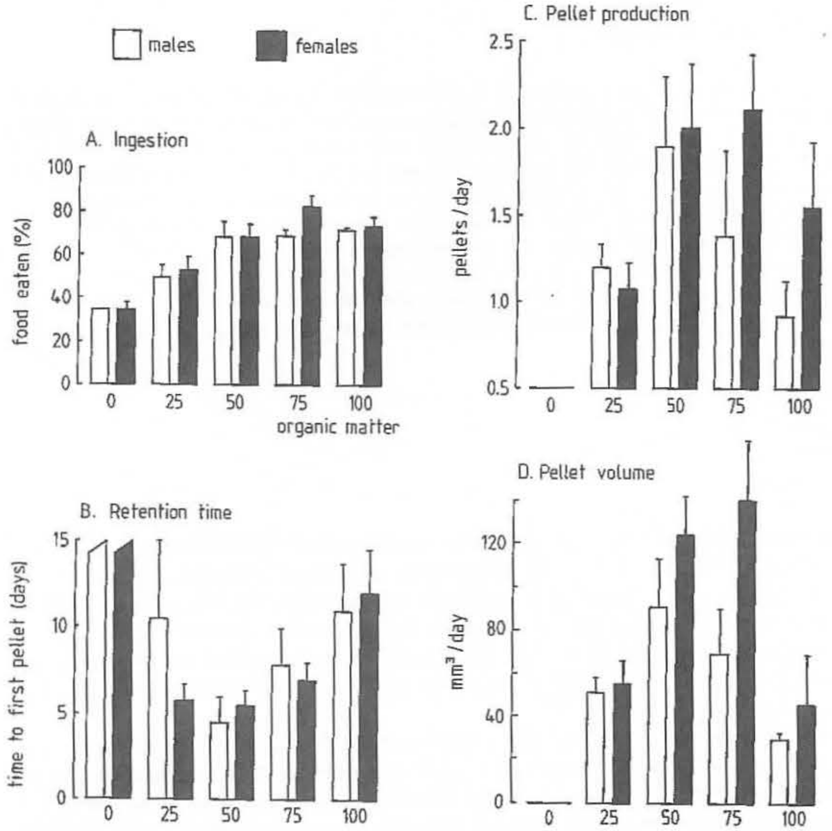

Fig. 1. Effects of five food treatments on (a) ingestion, (b) retention time, (c) pellet production rate and (d) volume of faecal material produced by male and female *Alloporus uncinatus* in a laboratory palatability experiment. All values are means ±1 S. E. and n = 14

Table 2. Analysis of covariance table for time to first pellet (days) produced by *Alloporus uncinatus* in five food treatments

Source	d. f.	SS	MS	F-ratio
Treatments	4	1022.86	255.71	19.31***
Sex	1	1.62	1.62	0.12^{ns}
Live mass	1	2.61	2.61	0.20^{ns}
Error	32	423.66	13.24	

Table 3. Analysis of covariance table for pellet production (pellets per day) by *Alloporus uncinatus* in five food treatments

Source	d. f.	SS	MS	F-ratio
Treatments	3	3.74	1.25	0.12^{ns}
Sex	1	0.04	0.04	0.07^{ns}
Live mass	1	0.88	0.88	0.23^{ns}
Error	28	16.19	0.58	

Females produced larger individual pellets than males (table 4) although this was only significant for the 50% organic matter food treatment (Mann-Whitney U-test, $U = 53.0$, $P < 0.05$). This effect contributed to a greater volume of faecal material being produced by females during the experiment (fig. 1 (d)). When pellet size was combined with production rate there were significant treatment, sex and body mass effects on the volume of faecal material produced each day (table 5).

Table 4. Two-way analysis of variance table for food treatment and sex effect on the mean size (mm^3) of *Alloporus uncinatus* pellets produced in the palatability experiment

Source	d. f.	SS	MS	F-ratio
Treatments	3	1954.93	651.65	3.91*
Sex	1	1235.58	1235.58	7.42*
Treatment x Sex	3	449.10	149.70	0.90^{ns}
Error	27	4498.90	166.63	

Table 5. Analysis of covariance table for pellet volume (mm^3 per day) produced by *Alloporus uncinatus* in five food treatments

Source	d. f.	SS	MS	F-ratio
Treatments	3	1480.51	493.50	3.88**
Sex	1	1081.33	1081.62	8.51**
Live mass	1	873.33	873.33	6.87**
Error	28	3557.48	127.05	

Food preference

The dry mass of food eaten (% of total) by males and females in the preference experiment is shown in fig. 2. The large standard errors are due to considerable between-individual variation in total ingestion and differences in preference. An analysis of rank order preference based on percentage of food ingested suggested a non-random selection of foods (Kendall coefficient of concordance; females $W = 0.793$, $P < 0.01$ and males $W = 0.591$, $P < 0.1$) with the 0% soil and 25% soil foods ranked 1 or 2 in 84% of cases. Preferences shown by males may be more variable than females, for example, one male of 9.74 g body mass ingested 27.2% of the mineral soil presented.

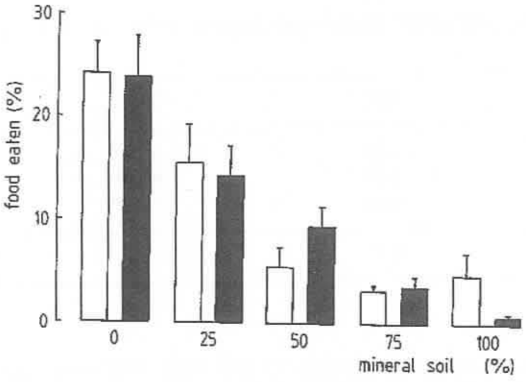

Fig. 2. Ingestion (percentage of food eaten) by male (open bars) and female (shaded bars) *Alloporus uncinatus* in a laboratory food preference experiment. n = 13 for males and n = 12 for females

Analyses based on actual dry mass ingested of each food showed no correlation between total dry mass of food ingested and body mass in males (Kendall rank correlation coefficient, $K = 0.128$, $P > 0.1$) or females ($K = 0.394$, $P > 0.1$). There was significant variation in mean dry mass of each of the five food treatments ingested by females ($F_{4,59} = 5.97$, $P < 0.001$) whilst greater ingestion by males of the 75% soil and 100% soil treatments resulted in no significant difference in ingestion of the different foods ($F_{4,64} = 1.12$, $P > 0.1$).

There was no correlation between retention time and body mass and the mean time (days ± 1 s. e.) to production of the first faecal pellet by females was 7.75 ± 1.21 not significantly different from 5.31 ± 1.37 in males ($U = 185.0$, $P = 0.121$). Higher ingestion rates only resulted in shorter retention times for females ($K = -0.707$, $P < 0.01$).

The number of pellets produced ranged from 0.50 to 3.30 day^{-1} and was positively correlated with the amount of food eaten in males ($K = 0.558$, $P < 0.05$) and females ($K = 0.869$, $P < 0.001$). There was no significant difference between males and females in pellet production rate ($U = 136.5$, $P = 0.301$). Three females did not produce pellets during the experiment although they ingested 0.67, 0.40 and 0.29 mg of dry food. The volume of individual pellets was positively correlated with body mass in males ($K = 0.806$, $P < 0.001$) and females ($K = 0.628$, $P < 0.01$).

Discussion

The proportion of ashed soil in the food had significant effects on ingestion, retention time and the volume of faecal material produced by *Alloporus uncinatus*. Body mass and the sex of the animal were also a source of variation. Despite considerable within treatment heterogeneity, treatment effects were significant with mixtures of soil and organic material resulting in more food being ingested and a greater volume of faecal material being produced at a faster rate. The proportion of soil in the food, body mass and sex of the animal can be added to temperature (Striganova, 1972), food quality (Neuhauser & Hartenstein, 1978;

Kheirallah, 1979; Striganova & Prishutova, 1990) and season (Pobozsny, 1986) as potential determinants of ingestion in millipedes.

The presence of mineral soil in the diet does seem to reduce retention time. Individuals that ingested only organic material retained this food for longer than those animals fed a mixture and longer than those in the preference experiment. This argument may be simplistic as further experiments have shown that starved animals often retain food in the gut and cease pellet production which is resumed, often at a rapid rate, when feeding starts again (Dangerfield, unpublished data).

Ingestion rate in the palatability experiment ranged from 0.023 to 0.030 grams per gram dry mass per day (g g^{-1} day^{-1}) except for the 100% organic matter treatment which averaged 0.016. These values are lower than the 0.034 in *Orthoporus ornatus* (Girard) (Wooton & Crawford, 1975) which is a smaller species than *A. uncinatus* and an upper value of 0.041 in *Sarmatiulus kessleri* (Lohmander) (Striganova, 1972). Similarly Pobozsny (1986) gives ingestion estimates for five temperate millipede species between 0.038 and 0.054. Another multispecies comparison using different foods gave much lower estimates of between 0.00016 and 0.0043 (Neuhausen & Hartenstein, 1978). Mass specific ingestion rates for *A. uncinatus* are comparable to those for temperate species even though at 8 – 10 g live mass, individuals are an order of magnitude larger than most temperature species.

All foods appeared at least partially acceptable to *A. uncinatus* including ashed soil. This was consistent with field observations of this species feeding on a wide range of materials including fallen fruits (*Uapaca kirkiana*, Muell. Arg.), mammalian faeces, leaf litter and mineral soil (Dangerfield & Telford, In Press). Although a wide range of foods appear palatable the proportions of each food type in the natural diet are not known. Most individuals selected ground leaf material in the preference experiment but as in other studies on the feeding behaviour of detritivores (Richardson, 1975; Rushton & Hassall, 1983) they appeared to sample all the food types available to the extent that in males there was no significant differences between treatments in the dry mass of foods eaten.

Selective feeding will not only influence the fitness of individuals (Hassall & Rushton, 1984) but also the role of the animal in decomposition processes and nutrient dynamics. At a field density of 1.0 m^{-2} and a period of surface activity of 111 days (Dangerfield & Telford, 1991) together with ingestion rates obtained in the present study, *A. uncinatus* would ingest 10.77 mg dry mass of leaf litter m^{-2} $season^{-1}$ and produce approximately 4.2 cm^3 of faecal material m^{-2} $season^{-1}$ if fed on leaf litter exclusively. If the leaf litter was mixed with mineral soil, potential consumption of leaf litter would decrease but the volume of faecal material would increase to 12.2 cm^3.

Given that the type of food eaten is an important determinant of the volume of faecal material produced, this can influence nutrient dynamics as larger pellets containing mineral soil appeared more friable than organic rich pellets. Large pellets would be less likely to persist in the environment and would potentially release nutrients sooner. The total nitrogen content (%) of faecal pellets was 0.54 to 1.2 times higher than in the experimental foods, with a similar pattern for total phosphorus (Dangerfield & Telford, 1989). Pellets may represent a concentration of nutrients in small units which are likely to be distributed throughout the environment. Little is known about the decomposition of detritivore faecal pellets (Nicholson, et al., 1966) and such studies might usefully be combined with those on feeding behaviour and population ecology to consider further the potential regulatory role of millipedes in decomposition and nutrient dynamics.

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